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The Rhythmic Activity of *Nautilus pompilius*, with Notes on its Ecology and Behavior in Fiji

by

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Abstract. Specimens of *Nautilus pompilius* were trapped on the sea floor in depths of 450 to 500 m off Suva, Fiji. As found in other studies, these were mainly mature (mean shell diameter 13.3 cm, range 10.3-15.2 cm; n = 74) males (90-94%). Eleven individuals were kept under simulated natural conditions (0.1 lux daylight intensity; 10-15°C) and activities were recorded constantly for a total of 80 days. Activity was characterized by bursts or periods of swimming (minor during the day; 5-12 min at night) every 30 to 50 min. These were termed "subcycles." Activity was crepuscular/nocturnal. Healthy, freshly collected specimens swam for an average of 160 min/day: 2.6 min/h during daylight, 11.9 min/h at dusk, 7.0 min/h during night, and 6.2 min/h at dawn (n = 4; 25 days of records). A rhythm comprising an innate subcycle of 30 to 50-min periodicity, modified by daily cycles of photoperiod, and an endogenous 24-h periodicity is proposed. Aquarium behavior is related to the natural habitat. It is proposed that the subcycles of activity are a strategy for hunting and scavenging in a homogenous environment where food is limited. *Nautilus* swam about 1600 m/day, of which most (1350 m) was at night. It is, therefore, unlikely that the population studied migrate at night to the nearest reefs (6000 m away) as suggested elsewhere. Brief notes are also included on the habitat, aquarium behavior, and growth rates of *Nautilus* in captivity.

INTRODUCTION

THE FOUR species of living *Nautilus* (SAUNDERS, 1981) are relicts of a large group of shelled cephalopod mollusks that flourished in the world's seas from the Triassic to the Tertiary, 225 to 65 million years ago. Because of the importance of the nautiloids and ammonoids in the fossil record, paleoecologists have shown considerable interest in establishing the ecology, behavior, and life history of living *Nautilus*, which are little known because of their deep water habitat and restricted distribution.

The present study investigates the activity patterns of *Nautilus pompilius* Linnaeus, a species found in depths of 100 to 650 m on reef slopes in the Philippines, Indonesia, New Guinea, Solomon Islands, possibly northeastern Australia, Vanuatu, and Fiji (WARD *et al.*, 1977; SAUNDERS, 1981).

A number of studies indicate that the *Nautilus* species are nocturnal. WILLEY (1902) suggested that they move up reef slopes from deepwater at night. BIDDER (1962) noted that captive *N. macromphalus* swam chiefly at night and spent most of the day at rest on the bottom. HAVEN (1972) described Philippine *Nautilus pompilius* as "diurnal" in activity, as only baited traps left overnight caught specimens. WARD *et al.* (1980) reported that the New Caledonian *N. macromphalus* had been observed swimming actively near the surface at night by divers, indicating that they are inactive during the day or migrate into deep waters. Carlson (DUGDALE, 1982 and personal communication) has evidence from specimens of *N. belauensis* released with telemeters that suggests that this species does move vertically, from 400 m to 100 m, at night.

Although specimens of *Nautilus* have been successfully kept in aquaria for periods of up to one year (JECOLN, 1980), there have been only superficial observations on their activity cycles. *Nautilus macromphalus* kept in aquaria in New Caledonia and Japan were reported to be active after sunset (MIKAMI & OKUTANI, 1977; JECOLN, 1980), and HAVEN (1972) noted that *N. pompilius* in aquaria in Philippines became active at dusk. HAYASAKA *et al.* (1982) made two days of visual observations on captive *N. pompilius*, and found they were most active at about dawn on both mornings. They concluded: "As far as our observa-

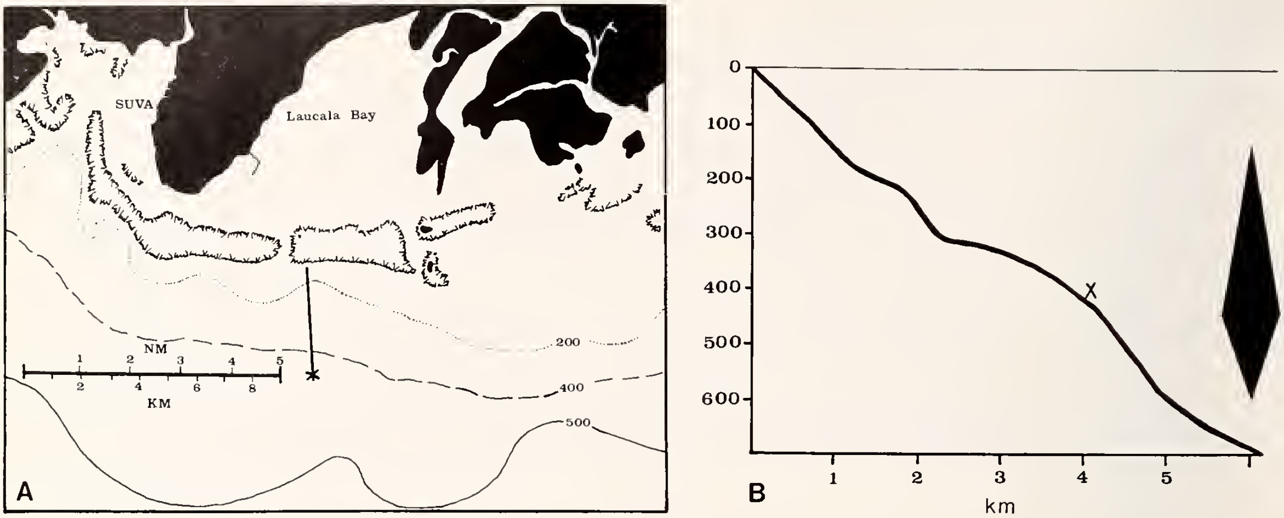

Figure 1

A. Collection site (x) off Suva Reef, Viti Levu Island, Fiji. B. Depth profile (meters) along transect in A, with kite diagram (arbitrary scale) of *Nautilus* distribution.

tions are concerned, it is hard to say that *Nautilus* is a nocturnal animal." A histogram of the data presented in Hayasaka *et al.* (1983) also shows some activity after sunset ("lights-off") and a major peak before dawn ("lights-on"); the authors considered that this activity may have been induced by the bright lights of the display aquarium.

In the present study, the swimming activity of 11 specimens of *Nautilus pompilius* held under simulated natural conditions of temperature and light was continuously monitored by activity recorder. Light and temperature regimes were also manipulated in an attempt to establish the nature of the rhythmicity. As little is known of the ecology or general behavior of *Nautilus,* some associated observations are also presented as a background to the study of swimming rhythmicity.

MATERIALS AND METHODS

Specimens of *Nautilus pompilius* were captured in chevron-shaped fish traps (1.80 × 0.9 × 0.6 m; conical entrance 20 cm in diameter) set on the sea floor at depths of 400 m to 500 m off Suva, Fiji (Figure 1). To determine whether *Nautilus* were leaving the bottom, four smaller traps were also placed at 20-m intervals from the bottom on the mooring line. The study site, 8 km south of the University of the South Pacific, was 4–5 km south of Nukubuco reef, and about 7 km east of the area where Ward *et al.* (1977) collected their *Nautilus.* Slightly decaying skipjack tuna was the most effective bait used. Initial surveys indicated that *Nautilus* was most abundant at 450–500 m. A total of 150 underwater photographs was taken of this area with a bottom-triggered Ewing deepwater camera.

Ninety specimens of *Nautilus* were obtained from eight trap series that were set at two to six week intervals between September 1982 and April 1983. Average catch per trap per day was 3.1 individuals (range 1.0–8.3). On each occasion two or three specimens were quickly returned to the laboratory in darkened containers of cooled seawater while other captives were either preserved or measured, tagged, and released. No recaptures were made.

Each *Nautilus* was held in a dark-sided, 100-L capacity aquarium of recirculating, charcoal-filtered and refrigerated seawater (10–14°C; salinity 34.5–35.5‰). The aquaria were kept in a darkroom that could be indirectly illuminated by a 15-cm diameter skylight with a 10 × neutral-density filter to further reduce light intensity. This illumination, of about 0.1 lux at mid-day and very dim to human eyes, approached that of natural conditions (0.004% of surface intensity of 470 nm light at 500 m). Artificial light, when necessary, was provided by indirect illumination from a 40-watt fluorescent light (approximately 2 lux). A red photographic safelight provided illumination when servicing the equipment in darkness. Disturbances were restricted to a daily instrumentation check and weekly feeding, cleaning, and water change. When available, several live deepwater carid shrimps, a possible prey of *Nautilus,* were left in the aquarium to provide a regular food source. At other times, *Nautilus* were fed on shrimp and fish during the day, although this tended to increase the duration of daytime activity.

Nautilus lived for up to three months under these conditions; they fed regularly and grew various amounts. However, all specimens became positively buoyant—they are usually neutrally buoyant—after several days of captivity.

Swimming activity was monitored directly and indi-

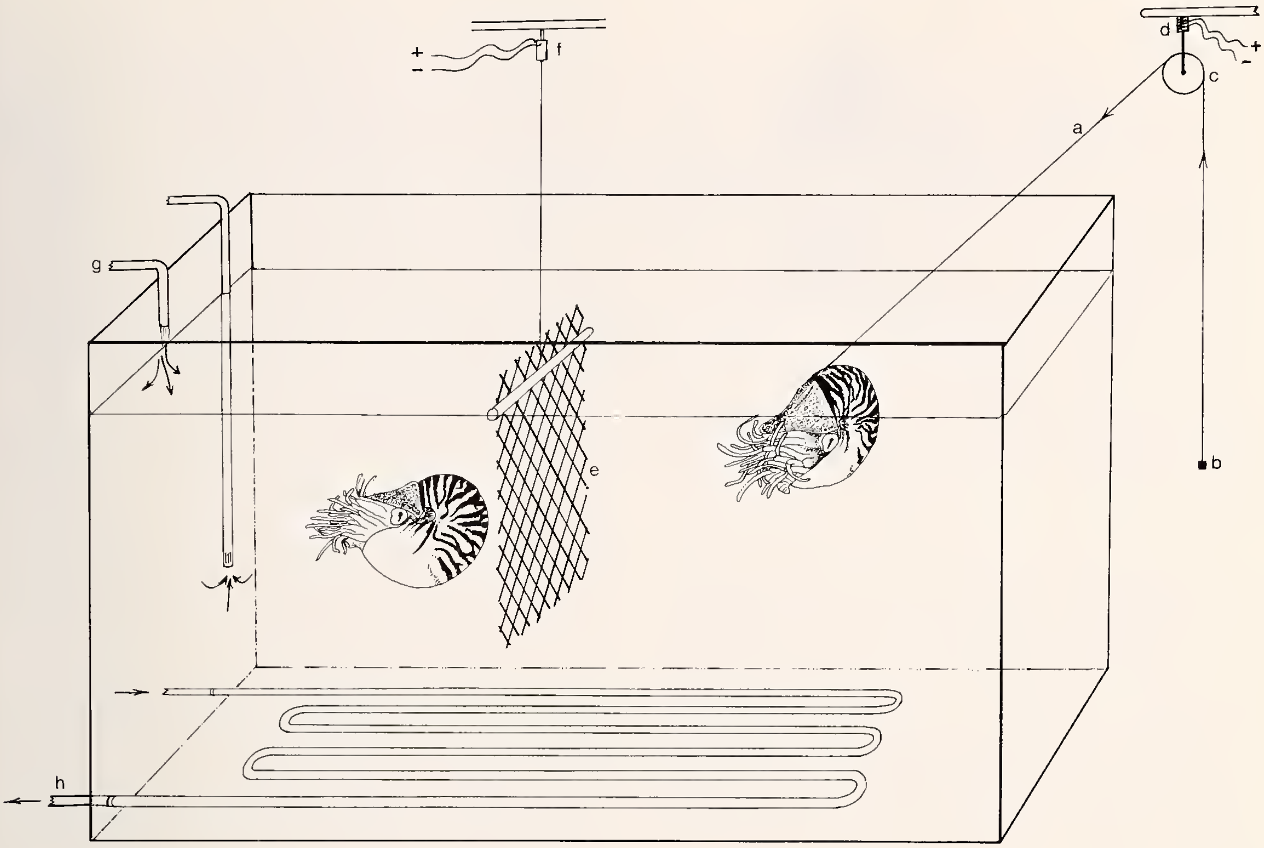

Figure 2

Activity recorders. Movements in a thread (a), counterweighted (b) and redirected by a pulley (c), were detected by a strain-gauge (d), amplified and recorded. Alternatively, a plastic wire panel (e) was suspended from a strain-gauge (f) that recorded a signal if touched by a swimming *Nautilus*. A single animal was placed in each dark-sided tank; water was constantly filtered (g) and cooled (h).

rectly. In the direct method, a cotton thread was glued with quick drying "Superglue"™ to the dorsal surface of the shell, and passed through a small pulley fixed above the aquarium to a light counterweight (1 to 2 g) which kept tension on the thread. An engineering strain gauge, fitted to the pulley, detected any slight movement in the system. A slow-speed (10 cm/h) chart recorder recorded an amplified signal. The behavior of the *Nautilus* did not appear to be influenced by the slight friction of the pulley and counterweight but, to test this, an indirect recorder was also used for several experiments. This consisted of a rectangular plastic wire panel, weighted at the bottom and equipped with a float at the top, directly attached by thread to the strain gauge. To swim from one end of the tank to the other, the *Nautilus* had to make contact with the panel. Small, local movements were not detected. Because of the possibility of changes in behavior resulting from acclimation to the artificial conditions and activity recorder, *Nautilus* were usually replaced by freshly collected specimens after one week.

RESULTS

General Ecology and Aquarium Behavior

The outer-reef slope of Suva barrier reef initially slopes steeply to about 200 m depth, then more gradually to 500 m at about 4–5 km from the reef (Figure 1A). *Nautilus* were trapped in shrimp traps between 100 and 600 m, and were most abundant at 450–500 m (King, personal communication). No *Nautilus* were ever trapped in the traps suspended above the bottom, indicating that they rarely if ever leave the sea floor. Underwater photographs of the sea floor showed a uniformly soft bottom of terriginous clays from the nearby Rewa River, highly bioturbated by polychaete and other burrowers. No *Nautilus* were seen in 150 frames, covering about 3000 m^2 of sea floor. Crustaceans trapped in this area included carid shrimps (*Heterocarpus*; *Plesionika*; *Parapandalus*), galatheids (*Munida*), majid crabs (*Myra*; *Hyastenus*), goneplacids (*Geryon*), portunids (*Carybdis*), homolids (*Homola*), several pagurids (*Parapagurus, etc.*), and panulurids. Several

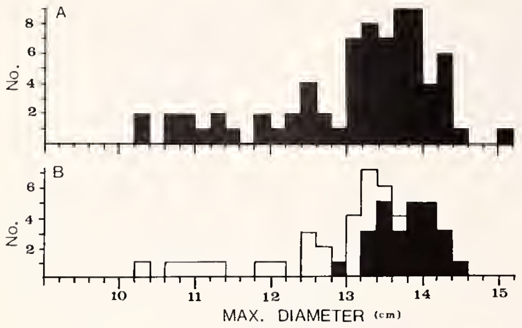

Figure 3

A. Size frequency distribution of *Nautilus* captured. These were collected from the same site over a 6-month period. B. Subsample of A, showing size of mature (black) and immature (white) specimens.

species of gorgonians, solitary corals, antipatharians, and hydrozoans, as well as a number of bivalves, gastropods, holothurians, ophiuroids, and echinoids were dredged from this area. A large number of species of fishes have been collected from the 100–600 m zone of Fijian reef slopes (Raj & Seeto, unpublished data).

Epizoites were present on some *Nautilus* shells. Clusters of between two and six of the small pedunculate barnacle *Temnaspis excavatum* (Hoek) were present on the umbos and ventral part of the shell, near the hyponome, of about 15% of *Nautilus* specimens. This barnacle has previously been recorded attached to isopods, crabs, and other barnacles from 200 to 400 m depths in the Indo-Pacific (Foster, personal communication). Isolated serpulid worm tubes were present on about 5% of specimens. On average, five of the ectoparasitic caligid copepod *Anchicaligus nautili* (Willey) were present on the shell and soft parts of each of ten *Nautilus* carefully examined.

The mean shell diameter of the *Nautilus* collected was 13.3 cm (mode 13.8 cm; range 10.3–15.2 cm; n = 74; Figure 3A). In the other studies of *Nautilus* off Suva, WARD *et al.* (1977) reported a mean diameter of 14.16 cm (n = 22) and TANABE *et al.* (1983) of 13.5 cm (n = 31). The shells of Fijian *N. pompilius* are variable in coloration. In about 60% of the shells, bands extended to the umbo and in the remainder they did not (termed variants A and B respectively by WARD *et al.*, 1977). Of 50 specimens dissected, three were females and two immature specimens were probably females—*i.e.*, only 6% to 10% were females. WARD *et al.* (1977) reported 14% females, and TANABE *et al.* (1983) reported 25% females in their Fijian studies. About half the sample examined (26 of 49) had definite eye notches, indicating their maturity. Notches appeared at 13.2–13.4 cm shell diameter, and all specimens above 13.8 cm had notches (Figure 3B). All studies of *Nautilus* since WILLEY's (1902) have found a similar anomalous predominance of males and an absence of juveniles, implying that the young and females either live in other habitats or are not prone to trapping. Little is known of the life-cycle of *Nautilus*.

Freshly captured *Nautilus* were gorged on fish bait (average gut contents 51 g; range 4–85 g; n = 10), and fed little for the first week. They subsequently consumed about 20–40 g of dead shrimp per week, showing a preference for the head.

Immature specimens kept for two months in the aquarium showed some growth. Individuals 11.6 cm, 12.1 cm and 13.1 cm in shell diameter added 3.6 mm, 2.7 mm and 2.2 mm respectively to the apertural margin per month. Note that this represents an increase of spiral circumference of about 1%, and there was little measurable increase in overall shell diameter.

Three of 45 living specimens examined had triangular bites out of the apertural margin matching the gape of a *Nautilus* jaw. HAVEN (1972) proposed that these are received in intraspecific fighting. One juvenile drift shell from Suva (5.5 cm in diameter) had a fresh bite from the margin, suggesting that these fights might sometimes be fatal or, alternatively, that smaller *Nautilus* may sometimes be eaten by larger *Nautilus* or squid.

The swimming behavior and tentacle positions were similar to those described by HAVEN (1972). When resting, *Nautilus* attached to a solid object with one or two tentacles, and slowly rocked to-and-fro with its respiratory pulses. This was regularly interrupted by a few seconds of minor activity and repositioning. When feeding, *Nautilus* extended its tentacles and swam forward in BIDDER's (1962) "cone of search," but at other times *Nautilus* swam backwards. During periods of slow swimming, usually of about 3 to 10 min in duration, the tentacles were either trailing or in HAVEN's (1972) "cat's whiskers" pose, and any obstacles in the aquarium were carefully avoided. *Nautilus* generally took several hours to learn the spatial arrangements of the tank, and became quite adept at avoiding the activity panel. When alarmed, and occasionally spontaneously, for no apparent reason, *Nautilus* swam very vigorously for 30 sec to 2 min, often colliding with the sides of the aquarium. Tentacles were usually shortened during flight.

Of 11 *Nautilus* examined, 6 individuals (Specimens No. 1, 2, 5, 6, 9, and 10) remained active and fed regularly during the duration of the experiments, from 4 to 36 days. Specimen No. 4 died on the sixth day of recording; No. 7 and 11 were moribund during the first two days of recording and were terminated, and No. 8 was highly stressed for the first two days of recording and moved continuously. It was noted that most specimens that became moribund had enlarged spadices. An autopsy on one specimen showed that a newly formed septum had fractured, and a sliver of shell had perforated the viscera.

Activity Rhythms

About 80 days of activity records from 11 mature male *Nautilus* were obtained; of these, about 20 days were dis-

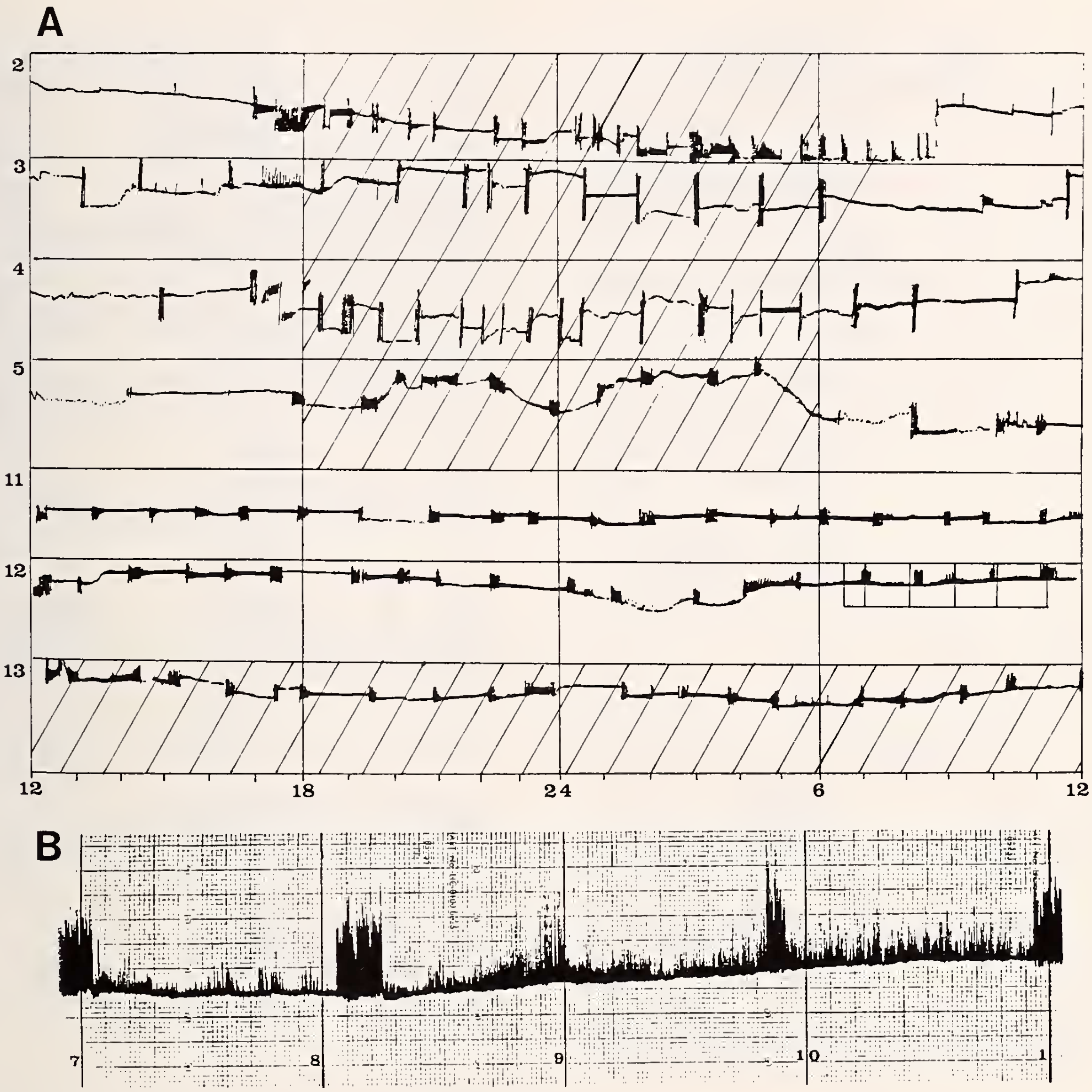

Figure 4

A. Actual records of activity of Specimen No. 1. Days 2 to 5 under normal photoperiod (L/D). Days 11 to 12 under constant light (L/L). Day 13 under constant darkness (D/D). Note subcycles of activity, especially under constant conditions. Differences in amplitude result from different gain settings on amplifier. B. Detail of recording for day 12. Horizontal axes: time in hours.

carded because of equipment malfunctions and erratic or moribund specimens. Malfunctions and power losses resulted in gaps of several hours in many records.

Records (Figure 4) clearly indicate the minor movements involved in position changing and the major movements of swimming activity above a thick baseline of electrical interference and shell rocking movements associated with the respiratory pulses. Activity was characterized by regular short periods or bursts of swimming of several minutes duration, followed by a longer period of inactivity. These are referred to as "subcycles" of activity. To determine whether the pattern of subcycles was a fatigue response due to the tethering to the activity recorder or to an innate pattern of activity, three *Nautilus* were tested in the panel activity recorder. These showed identical subcycles of activity and resting, indicating an innate behavior.

For analyses, the continuous records were arranged into hourly lots, and the duration of the swimming activity summed for each hour. The hourly activities of two *Nau-*

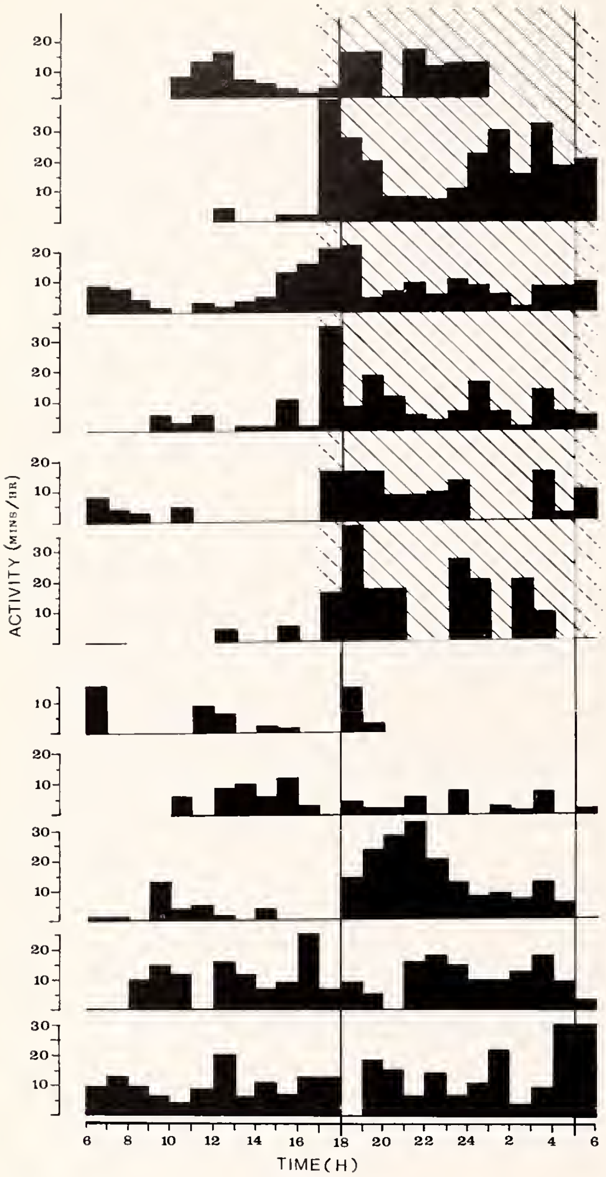

Figure 5

Summed activities for each whole hour, Specimen No. 1. Days 1 to 6 under normal photoperiod (L/D), days 7 to 11 under constant light (L/L). Shading represents night; dashed lines, dawn and dusk. Note nocturnal rhythm on days 2 to 6 (L/D) and on day 9 (L/L).

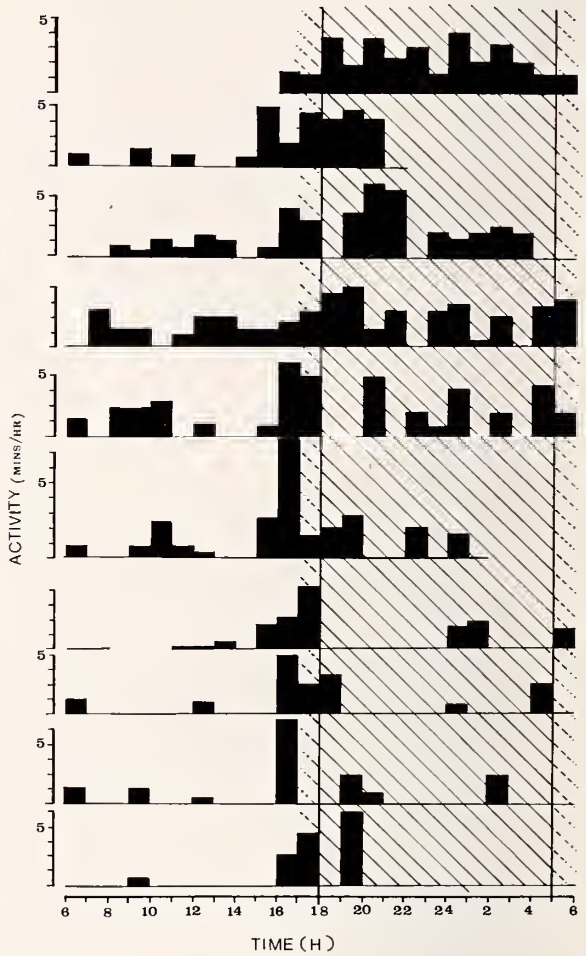

Figure 6

Summed activities for each whole hour, Specimen No. 9 (from partition recorder). The decline in activity after day 5 is partially due to an avoidance of the panel.

tilus over a total of 27 days are shown in Figures 5 and 6. Because the period of activity/inactivity was sometimes about one hour, hourly records may show alternate high and low activities, obscuring the general trend. Average activity for each hour of the day was therefore calculated to randomize sporadic activity or "noise," the subcycles, and the breaks in records. These show a pronounced nocturnal activity under "normal" photoperiod (Figure 7).

The activities of nine *Nautilus* over a total of 44 days are analyzed in Table 1. The average duration of swimming per day varied from individual to individual, with the moribund specimen (No. 4) and the two tested under the less sensitive panel activity recorder (No. 9 and 10) least active. *Nautilus* swimming activity averaged between 52 and 188 min/day, with the higher figures (170–188 min/day) the more credible because of those specimens' good health in the aquarium.

The duration of swimming activity quickly declined in the moribund specimen and gradually declined in the healthy specimens (Figure 6). The duration of activity on successive days of recording of *Nautilus* Specimens No. 1, 2, 5 and 6 are illustrated in Figure 8. After initially high activities on the first day of capture (due to the stress of capture and exploration of the new surroundings) activity declined to between 120 and 160 min per day. Activity increased in No. 6 on days 7 to 9, and in No. 1 on day 6, the days of, and following, feeding.

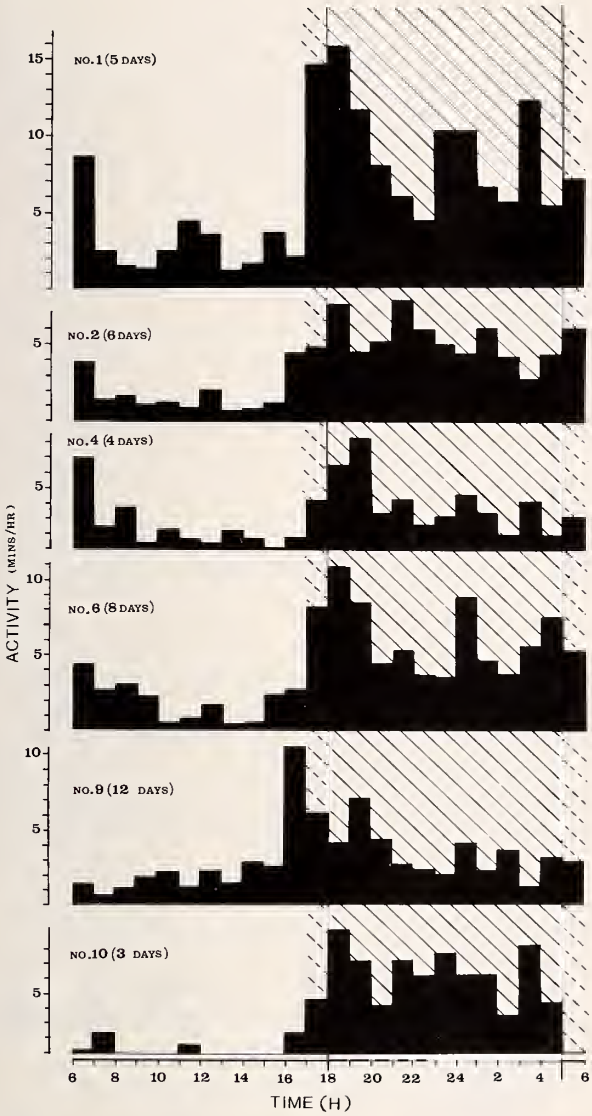

Figure 7

Average hourly activities of a number of days of recording (indicated) of six specimens. Note increased activity at dusk and anticipation of dusk in Specimens No. 2 and 9.

Under normal photoperiod, activity was lowest during the daylight hours (0700 to 1600) for all specimens on all days (average activities ranged from 0.9 to 3.0 min/h) (Figures 5 to 7; Table 1). Activity was highest at dusk (1600 to 1900) in all specimens (averages from 5.3 to 19.0 min/h) but continued throughout the night (averages from 2.3 to 9.3 min/h). Activity was not uniform during the night and several specimens showed three or four peaks of activity (including dusk) at about 4-h intervals. Dawn activity (0400 to 0700) was approximately similar to the nocturnal levels (averages from 1.1 to 8.7 min/h). Dusk activity often commenced before the actual dusk (*e.g.*, Specimen No. 9, Figure 6). On several occasions *Nautilus* were held under artificial light during the day, and dusk occurred as a sudden "lights-off." In most cases, activity preceded "lights-off" indicating that *Nautilus* anticipate dusk and are not stimulated to move solely by fading afternoon light.

To further test whether the nocturnal activity was an exogenous rhythm (controlled solely by environmental cycles) or an endogenous one (controlled by an internal or innate "biological clock"), Specimen No. 1 was placed under constant conditions after a period of normal photoperiod (Figure 5). Unfortunately, the record for the first night was lost due to equipment malfunction; day 2 of constant light showed random activity; day 3 showed a clear nocturnal rhythm; and days 4 and 5 showed random activity. This animal was later subjected to five days of constant darkness; hourly records showed uniform or random activity with the regular subcycles of activity predominating.

To determine the effects of temperature on the duration of swimming activity and on the general behavior of *Nautilus,* three specimens were subjected to a range of temperatures between 11 and 19°C (Figure 9). The average activities for each day (expressed as min/h) for two specimens were variable, while the other was more uniform. No specimens showed any increase in activity at the higher temperatures although this had been expected on metabolic grounds.

The subcycles of activity were relatively regular in their period from activity to activity, and in the duration of the activity, but they differed somewhat from individual to individual. The average duration of swimming in each subcycle of activity for the first three days of recording for *Nautilus* Specimens No. 1, 2, 5, and 6 was 6.7 min (individual averages ranged from 4.5 to 11.9 min; n = 300 measurements). The period of the subcycles, the time from the commencement of one activity to the commencement of the successive activity, averaged 41 min (individual averages ranged from 31 to 51 min; n = 300) (Table 1).

DISCUSSION

Nautilus held under simulated natural conditions were mainly nocturnal with a pronounced peak of activity at dusk. Their behavior was characterized by brief periods of swimming, followed by periods of inactivity or resting, at about 30 to 50 min intervals. These were termed "subcycles" to distinguish them from the 24-h rhythmicity. During the daylight hours the activity was minor, ranging from brief repositioning movements to a minute or so of slow swimming. During the night *Nautilus* alternately swam for between 5 and 12 min at a time and rested for about 20 to 40 min.

Under normal photoperiod (L/D) all the *Nautilus* examined were more active at night. Four freshly collected, healthy specimens tested over a total of 25 days were ac-

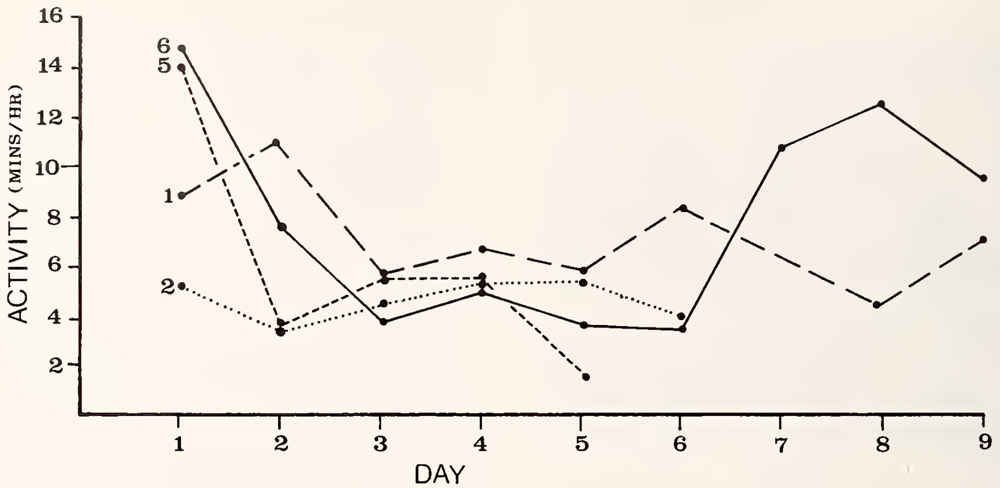

Figure 8

Daily activities (expressed as average activity in minutes per hour) of successive days of captivity for *Nautilus* Specimens No. 1, 2, 5, and 6.

tive for an average of 160 min/day. This period was not overtly affected by temperature (11–19°C range) although this might be expected on metabolic grounds. Their average activity during the hours of daylight was 2.6 min/h, at dusk 11.9 min/h, during the night 7.0 min/h, and at dawn 6.2 min/h.

The nocturnal rhythm did not persist under constant conditions of darkness (D/D) or light (L/L), but did reappear on one occasion after several days. However, because *Nautilus* regularly began moving an hour before dusk, before any decline in light intensity, the 24-h periodicity may be innate or endogenous.

The characteristic 5–12 min of activity each 30–50 min seen at night under normal photoperiod (L/D) continued for the entire 24 h under constant conditions of light (L/L) or darkness (D/D). This suggests that the subcycles of activity are a basic or innate behavior, modified by environmental factors (light and darkness) and a 24-h endogenous periodicity.

Several workers have previously alluded to the short-term periodicity, but did not comment on its significance.

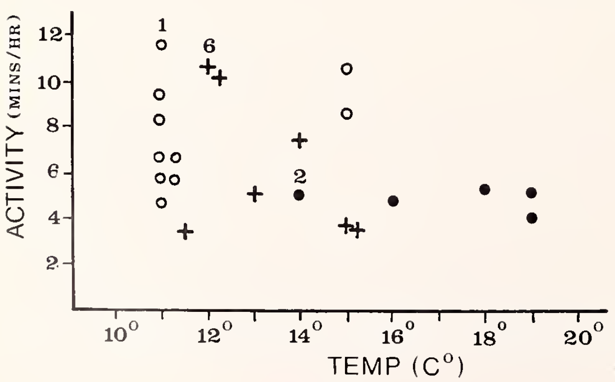

Figure 9

Daily activities (expressed as average activity in minutes per hour) of *Nautilus* Specimens No. 1, 2, and 6 at a range of temperatures.

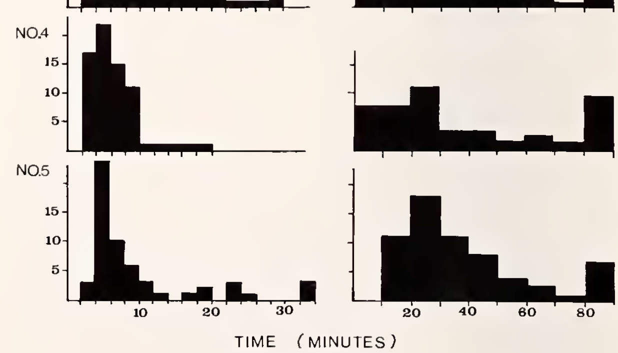

Figure 10

Frequency distributions of (A) duration of subcycle activity; (B) period from commencement of one activity to the commencement of the next, for the first three days of captivity of *Nautilus* Specimens No. 1, 2, 4, and 5.

Table 1

Analyses of activities of *Nautilus pompilius*.

	Nautilus specimen number								
	1	2	4	5	6	7	9*	10*	11*
Days recorded	1–6	1–6	1–4	1–6	1–9	1–2	1–8	1–3	1–2
Average temperature (°C)	12	16	19.5	15	12	21	13	14	18
(range)	(10–14)	(14–19)	(19–20)	(10–22)	(10–14)	(21–22)	(12–14)	(13–15)	—
Average activity per day (min)	172	111	52	172	188	188	96	67	170
(range)	(106–261)	(84–125)	(38–72)	(30–312)	(80–360)	(65–312)	(80–132)	(27–87)	—
Average activity (min) per hour of:									
Daylight	2.8	1.6	0.9	3.0	3.0	1.4	2.3	0.3	9.3
Night	9.3	6.7	2.3	3.7	8.5	7.7	4.0	5.0	14
Dusk	19.0	7.5	5.3	5.6	15.3	12.2	7.6	5.8	12
Dawn	6.1	4.4	3.2	5.5	8.7	8.3	1.7	1.1	17
Subcycles of nocturnal activity (min):								not analyzed	
Average duration of activity	11.9	5.7	2.5	4.9	4.5				
Average period from onset of activity to next activity	51	51	41	32	31				
Health in aquarium	good	good	poor: died	good	good	poor: moribund	good	good	poor: moribund
No. of days kept successfully in activity recorder	35 days	6 days	6 days	6 days	9 days	removed after 2 days	15 days	7 days	removed

* Recorded in panel activity recorder; others by direct attachment.

BIDDER (1962) stated that "from time to time an animal becomes restless and swims about until a new resting place is found" (presumably in the daytime), and HAYASAKA *et al.* (1983) observed that, over two days of visual observations, *Nautilus* "moved from 15–20 minutes and rested for 15–30 minutes repeatedly."

The alternating swimming/resting behavior may be a strategy for hunting and scavenging in the homogenous environment of reef slopes where food is scarce and intraspecific contacts infrequent. *Nautilus* is probably an opportunistic scavenger, evident from the gorged guts of the trapped specimens, and a carnivore, indicated by the regular feeding on live shrimps in the aquarium. Although underwater photographs showed a featureless soft bottom, no *Nautilus,* and few potential prey organisms, bait rapidly attracts a wide variety of species (KING, 1983).

A pronounced nocturnal rhythm in an animal living at a depth characterized by very low daylight intensity is anomalous, particularly because the "pin-hole camera" eye of *Nautilus* is far less sensitive to light, and of a far lesser visual acuity, than any lensed eye (HURLEY *et al.,* 1978). *Nautilus* may hunt using its olfactory sense at night, but its vision must be of some use during the daytime, a time when it is largely inactive. Alternatively, the eyes may be used for hunting caridian shrimps, one of the dominant animals of the reef slopes; these species are mainly nocturnal and release bioluminescent clouds when disturbed (KING, 1983).

From the aquarium studies of the duration of swimming and published estimates of velocity (average 0.17 m/sec; range 0.10–0.25 m/sec; WARD *et al.,* 1977), *Nautilus* would swim about 1600 m per day (260 m in daylight, 370 m at dusk, 670 m at night, and 200 m at dawn). This approximates some of the distances travelled by Carlson's telemetered *N. belauensis* (DUGDALE, 1982) which migrated into shallower waters at night. However, because of the distance to the nearest reef (6000 m) in this study, it is improbable that Fijian *N. pompilius* migrate in the same way.

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